## Alaska Fisheries Technical Report Number 77

# A Biological Assessment of Whitefish Species Harvested During the Spring and Fall in the Selawik River Delta Selawik National Wildlife Refuge, Alaska

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Key words: broad whitefish, *Coregonus nasus*, humpback whitefish, *Coregonus pidschian*, least cisco, *Coregonus sardinella*, Selawik River, salinity, otolith microchemistry, anadromous, GSI, spawning

November 2004

The U.S. Fish and Wildlife Service, Office of Subsistence Management, provided funding support for this project through the Fisheries Resource Monitoring Program, under project number FIS 03-016.

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The correct citation for this report is:

Brown, R. J. 2004. A biological assessment of whitefish species harvested during the spring and fall in the Selawik River delta, Selawik National Wildlife Refuge, Alaska. U. S. Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office, Alaska Fisheries Technical Report Number 77, Fairbanks, Alaska.

Abstract.—Whitefish (Family: Salmonidae, Subfamily: Coregoninae) are important food resources for residents of the Selawik River delta in northwest Alaska. Several species have been identified in the region but very little is known about their life histories. A biological sampling study was conducted during June and September 2003 to examine age and size distribution, maturity and spawning condition, the incidence of anadromy, and relative seasonal abundance of whitefish species found in the delta. Broad whitefish Coregonus nasus, humpback whitefish C. pidschian, and least cisco C. sardinella were abundant throughout the delta, and inconnu (sheefish) Stenodus leucichthys were present but relatively rare. More than 70% of the whitefish of all three major species were mature and most were actively feeding. Few juvenile fish were captured despite the use of suitable fishing gear. Age distributions were well beyond minimum age of maturity, indicating that recent harvest levels have not been excessive. A large proportion of mature broad whitefish and humpback whitefish, and all mature least cisco were coming into spawning condition during the September sampling period. Otolith microchemical procedures indicated that most broad whitefish and humpback whitefish were anadromous, while most least cisco were freshwater residents. Fish were more abundant in June than in September, but fish were in better physical condition during September. These data indicate that the Selawik River delta serves as a feeding area for these fish populations, and suggest that they spawn and rear elsewhere.

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#### Introduction

The Selawik River drainage and associated wetland and estuarine areas lie in northwest Alaska (Figure 1). Pacific salmon *Oncorhynchus* spp. have been documented in the drainage but they are not found there in abundance. As a result, local residents depend on other fish species in the area to meet their subsistence needs. Northern pike *Esox lucius*, burbot *Lota lota*, and several whitefish species (Family: Salmonidae, Subfamily: Coregoninae) are harvested throughout the region, with the combined harvest of whitefish thought to exceed all others (U.S. Fish and Wildlife Service 1993).

Five whitefish species have been reported in the Selawik River drainage. Inconnu (sheefish) *Stenodus leucichthys*, broad whitefish *Coregonus nasus*, and humpback whitefish *C. pidschian* are relatively large and are actively targeted in subsistence fisheries in the area. Least cisco *C. sardinella* and round whitefish *Prosopium cylindraceum* are relatively small. Least cisco are taken in the fishery, but are either less common than the larger species, or not as vulnerable to the fishing gear, as the reported harvest is much lower. Round whitefish are present in the upper reaches of the Selawik River drainage, but are not common in the fishery, which takes place in the delta (U.S. Fish and Wildlife Service 1993).

Management of a fishery for long-term sustainability requires an understanding of species life history, resource abundance, and population growth rate. Additionally, there must be some level of control over the exploitation rate. This understanding and control may exist in the Selawik and Kobuk rivers region for inconnu, but not for any of the other whitefish species. The story of how this information was gained for inconnu illustrates how complicated it can be to understand whitefish life history dynamics, and identifies many of the issues to consider when investigating other species, so it bears delving into briefly. Alt (1969) documented spawning migrations of inconnu into the Kobuk and Selawik rivers, and overwintering habitat in Hotham Inlet and Selawik Lake. Underwood (2000) used mark recapture techniques and estimated the inconnu spawning population in the Selawik River during 1995 and 1996 to be 5,190 and 5,157, respectively. Similarly, Taube (1996, 1997) estimated the inconnu spawning population in the Kobuk River during 1995 and 1996 to be 32,273 and 43,036, respectively. Subsistence, commercial, and sport harvests of inconnu are estimated annually and regulated by the Alaska Department of Fish and Game (ADF&G) (Brennan et al. 2002; Savereide 2002). Alt (1977) reported that some inconnu tagged in the lower Selawik River were recaptured in the Kobuk River, and suggested that the inconnu in the region were actually one large stock, rather than two discrete stocks. However, during the mid-1990s, when large numbers of inconnu were being tagged in their spawning areas in the Kobuk (Taube 1996; 1997) and Selawik (Underwood 2000) rivers, no mixing of stocks on the spawning areas was documented. Thus, Underwood (2000) proposed that Kobuk River inconnu ranged into the lower Selawik River to feed, but returned to the Kobuk River to spawn. Genetic analyses of inconnu from the two rivers supported the hypothesis that each river maintained a distinct spawning population with minimal gene flow between (Miller et al. 1998). Recaptures of tagged fish from both river systems in the winter fishery in Selawik Lake and Hotham Inlet, as well as Alt's (1977) tagging data, indicated that these stocks shared feeding and overwintering habitats. These complicated issues related to inconnu

migration and habitat use during seasonal periods or life history stages illustrate the difficulties inherent in describing population dynamics of all exploited whitefish species.

Limited harvest records suggest that 15,000 to 30,000 fish of all whitefish species combined are harvested in the lower Selawik River each spring (U.S. Fish and Wildlife Service 1993; Troyer, U.S. Fish and Wildlife Service, unpublished document). Georgette (2002) reported that major fishing activities occur in both spring and fall, but no quantitative records of fall harvests have been collected, so estimates of the total annual harvest of whitefish species in the Selawik River are not available.

Spring harvest records suggest that broad and humpback whitefish are more heavily exploited in the Selawik River delta than inconnu (U.S. Fish and Wildlife Service 1987, 1993). Yet our knowledge of their spawning, rearing, feeding, and overwintering habitats is almost completely lacking. Seasonal harvest data and discussions with local fishers have shown that whitefish of several species are present in the lower river and associated lake systems at almost any time of the year (Johnson 1986a; Georgette 2002). However, due to complex life histories, whitefish migrations are difficult or impossible to detect through localized harvests, so the presence of whitefish in the delta throughout the year does not imply the absence of fish migration. Johnson (1986b) attempted to locate spawning and overwintering habitats of humpback and broad whitefish using radio telemetry. The results suggested that long migrations were occurring for at least some fish. However, his success rate was low, and small sample sizes precluded population level inferences. If whitefish species in the Selawik River region exhibit similar patterns of behavior as those in other locations where they have been studied more thoroughly, migrations must be occurring between seasonally important habitats for all the fish stocks in the area. The following is a general summary of whitefish life history based on the literature.

Whitefish life history.—Whitefish living within river systems are thought to follow a generalized life history pattern as summarized by Reist and Bond (1988). Spawning takes place in the late fall in flowing water over a gravel substrate (Alt 1979). All whitefish species are broadcast spawners. Their eggs are cast into the water column where they drift downstream and sink to the bottom, becoming lodged in the interstitial spaces in the gravel (Scott and Crossman 1973; Morrow 1980). They develop through the winter, hatch in the spring, and emerge into the water column as the high flows of spring and early summer fill the waterways (Naesje et al. 1986; Shestakov 1991; Bogdanov et al. 1992). The tiny juveniles are carried downstream by the rapidly flowing water to a wide array of chance destinations that include backwaters along the river, offchannel lakes, and estuary regions at river mouths (Shestakov 1992). After several years of growth, young whitefish become mature and prepare to spawn. Beginning in midsummer, they migrate toward upstream spawning sites, during which time they reportedly do not feed (Alt 1969; Dodson et al. 1985). Major spawning areas appear to be used each year, so fidelity to natal spawning areas is thought to be high (Hallberg 1989). Following spawning, mature fish retreat downstream to overwintering locations (Alt 1979), and eventually to feeding areas by the following spring. Schmidt et al. (1989) found that overwintering whitefish in the extreme habitats of the Arctic coast of Alaska did little if any feeding regardless of food availability. It is unclear if whitefish in less extreme environments behave similarly.

Spawning is thought to occur every other year or even less frequently for most whitefish species (Reist and Bond 1988; Lambert and Dodson 1990). Minimum age of spawning maturity has been reported as young as age 3 or 4 for least cisco (Fleming 1996), age 4 or 5 for humpback whitefish (Fleming 1996), age 5 or 6 for broad whitefish (Alt 1976), and age 7 or 8 for inconnu (Brown 2000). Reported otolith age estimates for whitefish species range as high as 16 for least cisco (Bond and Erickson 1985), 57 for lake whitefish *Coregonus clupeaformis* (Power 1978), a species closely related to Alaskan humpback whitefish (McPhail and Lindsey 1970), 27 for broad whitefish (Babaluk et al. 2001), and 31 for inconnu (Howland 1997). Reist and Bond (1988) proposed that during the fall spawning period there are three main components of whitefish populations: immature fish far downstream of the spawning areas; mature nonspawners also downstream of the spawning areas but not necessarily in the same places as immature fish; and mature spawners at or near upstream spawning areas.

Whitefish in the Kotzebue/Selawik region.—Brennan et al. (2002) pointed out that in the Kotzebue region, whitefish escapements had not been monitored in the past because there had been no indication that populations were declining. Spawning migrations of one or more whitefish species other than inconnu have been reported or suspected in the Selawik, Kobuk, and possibly the Noatak river drainages (Alt 1979; Johnson 1986b; S. Georgette, ADF&G, Kotzebue, personal communication; T. Underwood, USF&WS, Fairbanks, personal communication). But specific spawning locations are undefined and no information on the sizes of spawning populations are currently available.

The development of a management plan for whitefish species other than inconnu would require more detailed knowledge of the distribution and abundance of spawning stocks. Spawning areas must be located, seasonal migration routes plotted, and overwintering and spring feeding habitats identified. Ideally, rearing areas would be identified as well.

Chang-Kue and Jessop (1992) found the same whitefish species assemblage in the Mackenzie River in northern Canada. They found that young fish were widely distributed in nearshore marine water and small coastal streams. When they matured they migrated hundreds of kilometers across marine water, through the delta, and far upstream in the Mackenzie River and its tributaries to spawn. It is reasonable to expect that seasonal and life history migration patterns for these species in the Kotzebue/Selawik River region are just as complex. And as with inconnu, the spawning areas may be the only locations where spawning stocks segregate. Obtaining this complex information for whitefish stocks harvested in the Selawik River drainage requires a series of carefully directed studies. The first step is to describe the species and life history stages currently present in the area.

R. Johnson and K. Troyer, both fisheries biologists with the USF&WS, documented the spring subsistence catches in the lower Selawik River during 1985, 1987, and 1993. A few informal reports were prepared from the data, and harvest estimates from the spring seasons were calculated based on their surveys. While these data were never formally published, a great deal of information was collected regarding the species harvested in the fishery, along with fork lengths of many hundreds of fish. These records were incorporated into this project and provide baseline data for comparison with current information to evaluate population-level changes in the fishery.

Goals of the 2003 sampling project.—The primary goals of this project were to identify the species composition of the spring and fall subsistence harvests in the lower Selawik River; compare the mean lengths of whitefish species captured in the 2003 spring subsistence fishery with those collected in 1985, 1987, and 1993; compare the median lengths, weights, and ages of spring 2003 samples with fall 2003 samples; estimate the spawning proportion of the fall 2003 samples; and conduct otolith microchemical analyses from a subsample of each species to evaluate patterns of marine versus freshwater habitat use. Secondary goals were to collect water temperature and salinity data from a number of locations in the lower Selawik River and associated lake systems.

#### Methods

Sampling and biological data collection.—Whitefish species in the Selawik River delta were captured by local subsistence fishers using gillnets of variable length with 10-cm to 15-cm stretch mesh, and through directed sampling with monofilament gillnets 15-m long with 5-cm and 10-cm stretch mesh. Fishing occurred during two 5-day sample periods in 2003; from June 16 to 20, and from September 15 to 19. Fish were sampled from many locations across the Selawik River delta in June and September. Total catch and catch per unit of fishing effort (CPUE) for all species combined, which was calculated as fish per net-hour, were recorded from the directed sampling. The CPUE values from the June sample period were compared using a Mann-Whitney test (Conover 1999) to those from the September sample period. The null hypothesis was that fishing effort was equally productive in both sample periods and that the median CPUE from June was equal to that of September. Significant differences were based on  $\alpha = 0.05$ .

Fish from the subsistence harvest and the directed sampling were examined. All fish species were identified and biological data were collected from whitefish. The fork length (length) of each fish was measured to the nearest 5 mm. All fish were weighed whole and egg skeins were extracted from females and weighed separately. The feeding condition was noted based on the presence or absence of food in the digestive tract. A Fulton condition factor, K, a means of evaluating the relative condition of fish (i.e., fat versus lean), was calculated following the methods of Anderson and Neumann (1996):

$$K = (weight/length^3) \times 100,000$$
.

This calculation was applied to data from each whitefish species and median values of June and September samples were compared using a Mann-Whitney test. Significant differences were based on  $\alpha=0.05$  in all cases. Assuming that whitefish in the Selawik River area feed very little in the winter, as in the findings of Schmidt et al. (1989) for more northerly whitefish, fish condition would be expected to improve between June and September (one-tailed test), as in the findings of Chang-Kue and Jessop (1992).

A Chi-square procedure (Conover 1999) was used to test the hypothesis that the proportional contribution of each whitefish species to the total whitefish catch was similar in 2003 to that in data gathered in 1985, 1987, and 1993. Significant differences were based on  $\alpha = 0.05$  in all cases.

In her work on the traditional knowledge of whitefish in the Selawik River delta, Georgette (2002) related the perspective of many fishers that whitefish species have always been abundant. If the populations of fish in the region are stable, as this perspective suggests, the fish sampled in the spring of 2003 should be similar in size to those sampled in previous years. Mean lengths for broad whitefish and humpback whitefish sampled in 2003 were compared with those from similar data collected in 1985, 1987, and 1993 using an ANOVA test (Mendenhall and Sincich 1996) and fork length distributions were compared between 2003 data and the earlier collections with Kolmogorov-Smirnov tests (Conover 1999). Significant differences were based on  $\alpha = 0.05$  in all cases.

In the June sampling event, pre-spawning, nonspawning, and juvenile fish were expected to be feeding in lower-river habitats. In the fall, though, the pre-spawning fish were expected to have migrated to spawning areas far upstream or distant from their spring feeding locations, leaving the nonspawning adults and juvenile fish behind (Reist and Bond 1988). It was considered likely that a change in size and age composition would be observed in fish sampled from the two time periods, in part because of spawning fish leaving, and in part because of expected growth over the course of the summer (Fechhelm et al. 1995). A Mann-Whitney test was used to compare median lengths, weights, and ages of fish collected in the spring with those collected in the fall. Additionally, a Kolmogorov-Smirnov test was used to compare seasonal sample distributions of lengths, weights, and ages. Significant differences were based on  $\alpha = 0.05$  in all cases.

Spawning readiness of fish in the fall harvest was judged based on gonadosomatic index (GSI) values of female fish (Bond and Erickson 1985) and by the presence of pearl tubercles in male whitefish (Vladykov 1970). Gonadosomatic index values were calculated as egg weight percentage of the whole body weight following the methods of Snyder (1983):

GSI = (egg weight/whole body weight) x 100.

The eggs of nonspawning whitefish remain small throughout the summer and fall (Lambert and Dodson 1990), while those of fish preparing to spawn increase rapidly from GSI values less than 3% in June to values greater than 10% by the fall spawning period (Bond and Erickson 1985). Male whitefish reportedly develop enlarged gonads as they approach spawning time (Lambert and Dodson 1990), but the basis for judging spawning condition from male GSI values is not well established and was not considered in this study. Whitefish of some species, however, develop pearl tubercles, which are bumps that form on the head and scales, as they prepare to spawn. Vladykov (1970) showed that the presence of pearl tubercles was diagnostic of spawning readiness in species closely related to humpback whitefish, and that they are more distinct on males than females. Whitefish preparing to spawn were expected to migrate from the Selawik River delta to upstream spawning habitats by late summer or fall. Nonspawning whitefish were therefore expected to dominate the fall sample. Using GSI data and the presence of pearl tubercles, the proportion of fish preparing to spawn in the fall-sampled population was estimated based on the binomial probability distribution.

Otolith aging and microchemistry.—In recent years, fisheries scientists have used trace element distribution within growth increments in otoliths to describe life history events and patterns of movement of many species. Laboratory experiments have shown that certain environmental conditions that a fish experiences, such as salinity or shifts in seasonal temperature, influence the chemical composition of their otoliths (Mugiya and Tanaka 1995; Secor et al. 1995; Farrell and Campana 1996). While great potential exists for examining a wide range of elemental markers that may confirm the presence or absence of a fish in a given location or habitat (Severin et al. 1995; Thorrold et al. 1998), the clearest results in the discipline have been the documentation of fish movements between marine and freshwater by examination of otolith strontium (Sr) distribution (Secor 1992; Babaluk et al. 1997; Tzeng et al. 1997; Brown 2000; Howland et al. 2001).

Strontium is a 2+ ion in solution and precipitates in otoliths, replacing calcium (Ca) ions in the mineral matrix, in proportion to its concentration in water (Radtke 1989; Fowler et al. 1995; Secor et al. 1995). Strontium concentration in water varies with salinity (Dietrich et al. 1980; Wells 1997), with ocean water worldwide relatively stable at about 8.1 ppm (Lide 1990), and freshwater systems variable, but generally close to 0.1 ppm (Rosenthal et al. 1970). Diadromous behavior places fish in both freshwater and salt water. Time periods during which a fish lived in these two environments can be deduced based on Sr distribution patterns within their otoliths.

A subsample of 12 otoliths per species from broad whitefish, humpback whitefish, and least cisco was selected for otolith microchemical analyses to evaluate patterns of anadromy in the region. Analytical samples were chosen randomly from within species, season, and sex groups so an equal number of male and female fish from June and September collections were examined. Otoliths were thin-sectioned (sectioned) in the transverse plane through the core (Secor et al. 1991), mounted on a glass slide, and ultimately polished on a lapidary wheel with 1 µm diamond abrasive in preparation for microscopic viewing and microprobe analysis. Each otolith section was approximately 200 µm thick, and growth increments could be clearly viewed with transmitted light (Figure 2). Annuli identification criteria followed basic descriptions by Chilton and Beamish (1982) and illustrations by Haas and Recksiek (1995). Otoliths selected for microchemical analysis were coated with a thin layer of conductive carbon.

A wavelength-dispersive electron microprobe (WD-EM) was used for microchemical analyses of otoliths in this study. Campana et al. (1997) demonstrated that WD-EM instruments were capable of precise and accurate measurement of otolith Sr concentration. The technology functions by bombarding points on a sample surface with a focused beam of electrons. Atoms within the material are ionized by the electron beam and emit x-rays unique to each element. Spectrometers are tuned to count the x-rays from elements of interest, in this case, Sr. The x-ray counts at each sample point are proportional to the elemental concentration in the material (Potts 1987; Reed 1997; Goldstein et al. 2003).

Strontium x-ray counts were collected from a series of points along a core (precipitated during the first year of life) to margin (precipitated just prior to the fish's death) transect for each otolith. The electron beam used for this procedure was 5  $\mu$ m in diameter and was operated at an accelerating voltage of 15 kilo-electron-volts (keV), and a nominal current of 20 nano-amperes (nA). Center-to-center distance between transect points was approximately 8  $\mu$ m. X-ray counts were collected for 25 s at each point.

Strontium x-ray counts were converted to estimates of Sr ppm concentration based on a regression equation relating the two measures, similar to the process described by Howland et al. (2001). Empirical criteria developed by Brown (2000) for determining if sampled material was precipitated in freshwater or salt water were used in this study. Essentially, Sr x-ray counts below 1,300 (approximately 1,750 ppm) were considered to be from freshwater and above 1,300 were considered to be from salt water.

#### **Results**

Seventeen different sites were fished in the Selawik River delta during the 2003 field season, 11 in June and 6 in September. Despite the smaller number of sites fished in the fall, the same general areas of the delta were fished in both seasons (Figure 3). The CPUE was significantly greater throughout the region in June (median = 7.07) than in September (median = 0.77) (P = 0.003). To achieve comparable seasonal catches, gillnets were fished for about 20 hours in June and 150 hours in September. Subsistence catches were not included in this analysis because net-hours could not be determined.

Water temperature and salinity were measured throughout the Selawik River delta in both June and September. Temperature was recorded at the surface and the bottom (or at a depth of approximately 3 m in deep locations) at all fishing sites. Salinity measurements were taken at the surface and the bottom in a selection of locations in the lower Selawik River and nearby areas of Selawik Lake. June water temperature ranged between 11°C and 16°C with most sites being 14°C to 15°C for both surface and deep water. Only one site in June was thermally stratified; at a depth of 3 m it was 11°C and on the surface it was 16°C. September water temperatures at all sites, both surface and deep water, were measured at either 4°C or 5°C. Salinity was less than 1 ppt (normal salt water is approximately 34 ppt) at all locations, indicating a freshwater environment.

Three hundred nineteen fish of eight species were examined during the 2003 field season in the Selawik River delta (Table 1). Four whitefish species were identified in the catch; broad whitefish, least cisco, humpback whitefish, and inconnu. These were the same four species identified in the Selawik River delta during previous studies (U.S. Fish and Wildlife Service 1987, 1993). Together, they made up a majority of the catch, accounting for 291 of the 319 fish. Broad whitefish and least cisco were most common, followed closely by humpback whitefish; only three inconnu were caught. Other species, in order of catch frequency, were northern pike, longnose sucker *Catostomus catostomus*, Arctic grayling *Thymallus arcticus*, and burbot.

The distribution of the four whitefish species among annual catches was significantly different between the four years for which data were available (P < 0.001) (Table 2). Broad whitefish have been numerically dominant every year. However, the collections in 1985, 1987, and 1993 were entirely from local harvests, which used largemesh gillnets only, minimizing the harvest of smaller fish such as least cisco. The collection in 2003 used local harvests for part of the sample, but both large- and smallmesh gillnets were fished equally during directed sampling events, increasing the relative harvest of least cisco and juvenile fish of other species. Sampling bias is therefore thought to be the reason for the observed difference in annual distributions of catch among species.

*Broad whitefish.*—Broad whitefish were the primary species harvested in the local fishery and were a dominant species in directed sampling activities as well (Table 1), making up approximately 40% of the sample in 2003. Ages ranged from 3 to 27 years, with a median age of 11 (Figure 4). Median ages and age distributions between June and September samples were similar.

Broad whitefish lengths overall were approximately normally distributed around a median of 475 mm, ranging from 275 mm to 560 mm. The youngest age classes were generally smaller than older fish, but there was a high degree of overlap among length and age categories (Figure 5). Comparisons of mean lengths and length distributions revealed that broad whitefish captured in June 2003 were significantly larger those captured in 1985, 1987, and 1993 (P < 0.001 for both tests and all comparisons) (Figure 6). The average length for broad whitefish in 2003 was 456 mm compared to approximately 420 mm in 1985, 1987, and 1993. Median lengths and the distribution of lengths of broad whitefish collected in September were significantly greater than those collected in June (P < 0.001 for both tests).

The median weight of all broad whitefish sampled in 2003 was 1,201 g and ranged from 235 to 2,300 g. Fish collected in September were significantly heavier (median = 1,450 g) than those collected in June (median = 1,081) (P < 0.001 for both tests). A comparison of median Fulton condition factors from June (median = 1.174) versus September (median = 1.301) revealed a significant rise (P < 0.001). Regressions of the Fulton condition factors by age indicated that older fish in both seasons had lower values than younger fish (Figure 7). These data, combined with similar age distributions for June and September collections, suggest that growth and improved condition over the course of the summer were responsible for larger fish observed in the fall, rather than a demographic change in the population.

The GSI values for female broad whitefish in June were uniformly less than 3%, and in September were bimodal with a component less than 3% and another group that ranged between 14% and 20%. Female broad whitefish in the fall ranged from 5 to 19 years old, and from 275 mm to 560 mm in length. The GSI values plotted against age and length revealed that minimum age and length at maturity were 8 years and 445 mm respectively (Figure 8). All female broad whitefish younger than 8 years and smaller than 445 mm, or 8 years old with low GSI values, were considered to be immature fish, while those with low GSI values that were older than 8 years and larger than 445 mm were considered to be mature nonspawners. Based on these criteria, 7 fish were immature, 11 were mature nonspawners, and 12 were spawners. It was therefore estimated that  $52\% \pm 21\%$  (95% CI) of mature female broad whitefish in the delta during September were preparing to spawn. Males did not exhibit pearl tubercles but had similar age and length distributions, so it was thought that the same three life history stages were represented for them as well.

Of the 116 broad whitefish examined in 2003, 100 were found to be feeding, while only 16 were not. There was no apparent pattern between feeding condition and season, age, sex, size, or GSI.

Microchemical examination of the otoliths of 12 broad whitefish revealed that most had frequented marine water during one or more years as young fish. The Sr concentration levels in 11 of 12 fish rose unambiguously to levels indicating migration

into marine water, and only 1 fish appeared to remain in freshwater throughout its life (Figure 9).

Humpback whitefish.—Humpback whitefish were the secondary species harvested in the local fishery, which was similar to harvest records from previous years. When the catch from directed sampling activities were considered though, humpback whitefish dropped to third in relative abundance behind broad whitefish and least cisco (Table 1), probably because of the increased capture efficiency of least cisco with the smaller-mesh gillnet. They were relatively abundant in June and noticeably rare in September. Humpback whitefish made up approximately 22% of the sample in 2003. Ages ranged from 4 to 27 years, with a median age of 13 (Figure 10). The median age of September samples (median = 13 years) was greater than from June samples (median = 12 years), but not significantly so (P = 0.108). Comparison of seasonal age distributions was not performed because of the small September sample (n = 12).

Humpback whitefish lengths overall were approximately normally distributed around a median of 395 mm, ranging from 225 mm to 495 mm. The relationship between length and age was most noticeable for small and young fish, and once larger size was attained there was a high degree of overlap among length and age categories (Figure 11). Comparisons of mean lengths and length distributions revealed that humpback whitefish in 2003 were significantly smaller than those examined in previous years, averaging 383 mm in 2003 compared to 393 mm in 1985, and approximately 410 mm for both 1987 and 1993 (P < 0.001 for mean length comparison; for comparisons of length distributions, 2003 to 1985: P = 0.045, 2003 to 1987: P < 0.001, and 2003 to 1993: P = 0.004) (Figure 12). Median lengths of humpback whitefish collected in September (median = 410 mm) were greater than those collected in June (median = 390 mm) but not significantly so (P = 0.080). Comparison of seasonal length distributions was not performed because of the small September sample (n = 12).

The median weight of all humpback whitefish sampled in 2003 was 680 g and ranged from 112 to 1,210 g. Fish collected in September were heavier (median = 710 g) than those collected in June (median = 642), but not significantly so (P = 0.074). Comparison of seasonal weight distribution was not performed because of the minimal September sample (n = 12). Median Fulton condition factors were similar in June (median = 1.077) and September (median = 1.048).

The GSI values for female humpback whitefish in June (n = 24) were low, ranging between 0.4% and 4.8%, and in September (n = 5) were bimodal with three fish less than 3% and two fish greater than 16%. Female humpback whitefish in the September (n = 5) ranged from 13 to 27 years old, and from 385 mm to 495 mm in length. Based on age data, it was assumed that these fish were all mature, three nonspawners, and two spawners. In addition to the females captured in September, seven male humpback whitefish were captured as well. All the males were covered with pearl tubercles, distinct bumps along scale rows and their heads (Figure 13), an indication that they were preparing to spawn (Vladykov 1970). Pearl tubercles were also present on the two females with high GSI values but were not as distinct and wide-spread as on the males. Minimum age and length of all humpback whitefish that were known to be mature and preparing to spawn were 9 years and 380 mm, respectively; however, these values do not necessarily reflect population minimums because the sample was too small

to be representative. Similarly, it was clear that some mature humpback whitefish were not preparing to spawn, but it was not possible to suggest a spawning proportion because of the small sample size.

Of the 65 humpback whitefish examined in 2003, 40 were found to be feeding, and 25 were not. The three females from the September samples that were not preparing to spawn were feeding, and the nine fish that were preparing to spawn were not feeding. Other than the spawning condition in the fall there was no apparent pattern between feeding condition and age, sex, or size.

Microchemical examination of the otoliths of 12 humpback whitefish revealed that most had frequented marine water during one or more years. The Sr concentration levels in 11 of 12 fish rose unambiguously to levels indicating migration into marine water, and only 1 fish appeared to remain in freshwater throughout its life (Figure 14). Most humpback whitefish that went to marine water, went repeatedly throughout their lives.

Least cisco.—Least cisco were rarely harvested in the local fishery but were the second most abundant species in directed sampling activities (Table 1), making up approximately 37% of the sample in 2003. They were probably the most abundant species in the area because broad whitefish were vulnerable to large- and small-mesh gillnets, while least cisco were caught primarily in the small-mesh gillnets. Hence, the effective net hours of effort for least cisco were approximately half those for broad whitefish. Ages ranged from 2 to 16 years, with a median age of 6 (Figure 15). Median ages and the distribution of ages of least cisco collected in September were significantly greater than those collected in June (P = 0.012 for median age comparison; P = 0.003 for age distribution comparison).

Least cisco lengths were approximately normally distributed around a median of 300 mm, ranging from 200 mm to 410 mm. In general, older fish were larger, but there was a high degree of overlap among length and age categories (Figure 16). Median lengths and the distribution of lengths of least cisco collected in September were significantly greater than those collected in June (P < 0.001 for both comparisons).

The median weight of all least cisco sampled in 2003 was 294 g and ranged from 80 to 830 g. Fish collected in September were significantly heavier (median = 350 g) than those collected in June (median = 229) (P < 0.001 for both comparisons). A comparison of median Fulton condition factors from June (median = 1.084) versus September (median = 1.172) revealed a significant rise (P < 0.001). Regressions of the Fulton condition factors by age indicated that older fish in both seasons had higher values than younger fish, and that younger fish were in similar condition in June and September (Figure 17). The seasonal increases in length, weight, and Fulton condition factor suggest that growth and improved condition were at least partly responsible for the larger fish observed in the fall. The significant seasonal rise in median age suggests that some demographic change may have occurred as well.

The GSI values for female least cisco in June were uniformly less than 3%, and in September ranged from less than 1% to almost 19%. There were two fish with GSI values less than 1% and they were not preparing to spawn. Based on data presented by Bond and Erickson (1985) and Lambert and Dodson (1990), it was deduced that a group of 19 fish with GSI values ranging from 8% to 19% were all preparing to spawn. Female

least cisco in the fall ranged from 3 to 11 years old, and from 235 mm to 410 mm in length. The GSI values plotted against age and length revealed that minimum age and size at maturity were 5 years and 275 mm, respectively (Figure 18). All female least cisco 5 years old or older, which were also 275 mm or longer, were preparing to spawn. These data suggest that mature least cisco spawn every year.

Of the 108 least cisco for which feeding data were collected in 2003, 66 were found to be feeding and 42 were not. Approximately half of all female least cisco preparing to spawn in the fall were feeding. There was no apparent pattern between feeding condition and season, age, sex, size, or GSI.

Microchemical examination of least cisco otoliths revealed that only 3 of 12 fish had been to marine water, and 9 appeared to remain in freshwater throughout life (Figure 19). Strontium concentration levels in the otoliths of anadromous least cisco were much lower than those of anadromous broad whitefish and humpback whitefish, suggesting that they remained in an environment lower in salinity than did the other species.

#### **Discussion**

Broad whitefish, humpback whitefish, and least cisco were captured throughout the Selawik River delta during sampling activities in 2003. The CPUE data indicated that they were much more abundant in June than in September. Hilborn and Walters (1992) cautioned that CPUE data are proportional to abundance only if sampling effort is random with respect to the fish, which is why catch data from fisheries are generally not usable. The sampling in this study was not truly random, but it was widely distributed (Figure 3) without regard to fish abundance. The CPUE data are therefore thought to be a valid relative measure of seasonal abundance, which supports the conclusion that there were fewer fish in the delta during September than in June.

Understanding that there were fewer fish in September than in June does not explain why fish abundance changed. One possibility is that fishery harvests early in the summer resulted in reduced abundance later. This is considered unlikely because for long-lived species such as whitefish, heavy fishing pressure would act to reduce the frequency of older age classes (Healey 1975), a situation referred to as "growth overfishing" (Hilborn and Walters 1992). The similarity of seasonal age distributions for broad whitefish, the presence of older humpback whitefish in the September sample, and the seasonal increase in age distribution of least cisco, all suggest that fishing was not the cause of the seasonal decline in CPUE. The most likely explanation is that a substantial portion of the population migrated out of the area, becoming unavailable to the fishery.

Fish may leave a particular location for a variety of reasons that may include water temperature, food availability, seasonal habitat changes, or spawning. Spawning for whitefish species occurs in late fall or early winter (Reist and Bond 1988), and has been documented most frequently in flowing water over a gravel substrate. This type of habitat is not apparent in the Selawik River delta. Inconnu in the region migrate far up the Selawik (Underwood 2000) and Kobuk (Taube 1996; 1997) rivers to their spawning areas. Chang-Kue and Jessop (1992) conducted tagging studies with broad whitefish, lake whitefish, and least cisco in and near the Mackenzie River drainage and documented major migrations of whitefish from estuarine feeding and rearing areas to distant

spawning locations. It is likely that whitefish species in the Selawik River delta make similar migrations.

The GSI data presented earlier provided age or size guidelines for assessing maturity in these species, and while they were not absolute, they did allow a general assessment of the proportional presence of mature and immature fish of each species. It appeared that most broad whitefish age 8 or older and 445 mm or longer were mature, and those younger or smaller than this were immature. Based on these criteria of age and size at maturity, the total catch of broad whitefish during 2003 was composed of approximately 80% mature fish. Chang-Kue and Jessop (1992) reported that some age 7 broad whitefish, corresponding to a length of approximately 377 mm, were mature in a coastal stream near the Mackenzie River mouth in northern Canada. Their sample for evaluating maturity was almost 600 fish, and it is possible that if as many fish had been examined in the Selawik River delta younger and smaller mature fish would be detected as well.

The age criterion for determining maturity in humpback whitefish was not considered to be valid because of the small sample size in September. However, the smallest mature fish was 380 mm, and it was thought that this length criterion for maturity was reasonable. Fleming (1996) determined that the minimum length at maturity for a spawning population of humpback whitefish on the Chatanika River in interior Alaska was 328 mm for males. Two females that were 367 mm and 370 mm, respectively, were found to be immature based on their gonad development. Chang-Kue and Jessop (1992) determined the minimum length at maturity of spawning migrants in the Mackenzie River delta to be 350 mm. Using the conservative length criterion for maturity of 380 mm or longer it was estimated that approximately 72% of the humpback whitefish during 2003 were mature.

Least cisco appeared to be mature by age 5, which corresponded to a length of at least 275 mm. Similar to our findings, Fleming (1996) determined that the minimum length at maturity for a spawning population of least cisco on the Chatanika River was 263 mm for males and 283 mm for females. Chang-Kue and Jessop (1992) reported that age 5 least cisco, corresponding to a length of about 280 mm, were mature in their study area near the Mackenzie River mouth in northern Canada. Using criteria for maturity of age 5 or older or 275 mm or larger, it was estimated that approximately 82% of the least cisco during 2003 were mature. These data indicate that most fish of all three species captured in the delta were mature, and it is reasonable to expect that a large component of them would have been migrating to spawning areas during the September sampling period, accounting for the reduced abundance observed at that time.

Fisheries scientists frequently encounter situations where major components of fish populations, such as juveniles, spawners, or specific age classes, are missing from a sample (Healey 1975). Sometimes the issue involves the effectiveness of the sampling gear for a particular size fish. Environmental conditions may affect the distribution and survival of entire year classes of fish, leaving gaping holes in age distribution plots (Fechhelm and Fissel 1988). Other times missing fish are simply elsewhere.

Habitat preferences of juvenile whitefish have been particularly difficult to define. Alt (1969) searched with minimal success for young inconnu from populations in the Kobuk and Selawik rivers. Bond and Erickson (1985) and Chang-Kue and Jessop (1992), who conducted studies of whitefish species in the Mackenzie River delta in

northern Canada, found that immature fish dispersed widely in small coastal drainages and nearshore marine waters, while mature individuals were primarily associated with the larger river systems. In this study, juvenile fish were essentially absent from the samples. The 5-cm stretch mesh gillnet was selected for use because it is effective with whitefish of all species as small as 20 cm in length. Whitefish of this length can be as young as 1 or 2 years old, which would be immature for all species. Very few fish of this size range were captured for any of the three primary whitefish species, and only a small percentage of the total catch of any species were judged to be immature. These data indicate that most immature fish of all species were not present in the Selawik River delta during the 2003 sampling events, and were probably distributed farther west and north in Selawik Lake, Hotham Inlet, and the nearshore waters of Kotzebue Sound (Figure 1) in habitats similar to those used by the Mackenzie River populations.

Otolith microchemical technology has recently become available to fisheries scientists and provides a means of determining whether a fish has migrated between marine and freshwater. Application of this technology to whitefish species encountered during this study revealed that most broad whitefish (Figure 9) and humpback whitefish (Figure 14), and some least cisco (Figure 19) captured in the delta had lived in brackish or marine water. Salinity testing in this study showed that the Selawik River delta was a freshwater environment, at least during the summer, so fish would need to travel beyond the mouth of the river towards the sea to encounter salt water and obtain the elevated levels of otolith Sr that were observed. At this point it is not clear how far that would be. In the far northern part of Hotham Inlet, near the mouth of the Noatak River, winter salinities have been measured at 2 to 3 ppt just under the ice, and 15 to 23 ppt at 1 m depth (C. Lean, National Park Service, Nome, personal communication). Salinity records are not available for northwestern Selawik Lake or southern Hotham Inlet. Finding the location where salt water begins, which may vary seasonally, will only establish a minimum distance fish would have had to travel to obtain elevated levels of otolith Sr.

An examination of broad whitefish and humpback whitefish age distributions (Figures 4 and 10, respectively) revealed periodic patterns of age class abundance and scarcity. These patterns were considered to be real because there were relatively high sample numbers for both species (Table 1). For broad whitefish, ages 8, 12, and 16 appeared to be strong, and ages 10 and 15 were weak (Figure 4). For humpback whitefish, ages 6, 13, and 16 appeared to be strong, and ages 11 and 15 were weak (Figure 10). Additionally, it was remarkable that there were 3 age 27 humpback whitefish and 1 age 27 broad whitefish at the far upper age range for both species.

Not enough is known about the effects of environmental variables on whitefish survival at various life history stages to identify specific reasons for such patterns to emerge, but there are a number of reasonable possibilities. Underwood et al. (1998) implanted radio tags into inconnu migrating into the upper Selawik River to spawn in 1994. Approximately 60% of radio-tagged fish left the system during an extreme high water event prior to spawning time and failed to return. By contrast, radio-tagged fish in 1995 and 1996, years in which no fall high water events occurred, migrated into the spawning areas during spawning time at rates of 94% and 79%, respectively. These data suggest that floods prior to or during spawning season may reduce spawning success of whitefish. Low winter flows and cold winter temperatures may compromise a large portion of developing eggs on spawning grounds, as described by Salo (1991) for chum

salmon *Oncorhynchus keta*. Wood (1987) estimated that common merganser *Mergus merganser* broods foraging in streams on Vancouver Island consumed 24% to 65% of the coho salmon *Oncorhynchus kisutch* smolt produced in the systems, suggesting that unusually high populations of avian or aquatic predators following the emergence of juveniles in the spring may significantly affect age class survival. Storms or ocean currents may influence juvenile dispersal in marine coastal environments, as has been documented with Arctic cisco *Coregonus autumnalis* along the Beaufort Sea coast (Fechhelm and Fissel 1988). Any of these phenomena could affect large components of age 0 fish. Environmental effects on older fish would be expected to spread across multiple age classes and should not manifest themselves in specific low age classes as observed here.

It has been reported that whitefish species stop eating for a period of weeks or months prior to spawning (Alt 1969; Dodson et al. 1985; Brown 2000), which could be diagnostic of spawning condition for some species if it were found to be consistently true. Considering only the fall sample, the hypothesis that non-spawners were feeding and spawners were not did not hold true for broad whitefish or least cisco, but was true for the small sample of humpback whitefish. Feeding behavior of whitefish as they approach spawning time may be species- or habitat-specific, and will be examined further in future years.

Seasonal size differences for broad whitefish and least cisco are consistent with expectations of individual growth during the summer, resulting in population level increases in size. Fechhelm et al. (1995) documented similar population level increases in weight and length (which they converted to a relative condition factor) for broad whitefish in the Prudhoe Bay region of Alaska. Chang-Kue and Jessop (1992) used the same Fulton condition factor as in this study and also documented a seasonal increase in condition for all three whitefish species they examined in a small coastal stream near the Mackenzie River in northern Canada. These data, along with the observation that most fish of all species were actively feeding, indicate that the Selawik River delta is important feeding habitat for populations of mature broad whitefish, least cisco, and humpback whitefish.

Comparisons of length distributions of broad whitefish and humpback whitefish from this study to those of previous collections in the Selawik River delta revealed significant differences that probably reflect shifting harvest patterns over time for broad whitefish and differences in fishing gear for humpback whitefish. Only the June broad whitefish samples from the 2003 season were used in the comparison because samples from previous years were collected only in the spring. Broad whitefish in June 2003 were larger than those collected in previous years (Figure 6). Healey (1975) presented data showing that older age classes were eliminated from heavily exploited whitefish populations in Canada, and that the average size of fish was less in exploited populations than in unexploited populations. Harvest records in the Selawik River delta are not sufficiently detailed to compare annual harvest rates. But the size data presented here suggest that there has been a regional recovery from a time period when harvest rates were substantial enough to reduce the occurrence of larger broad whitefish, which includes the older age classes, from the population.

The situation for humpback whitefish was somewhat different, because the length distribution included a component of smaller fish that was not observed in previous years

(Figure 12). The length distributions for all four years in which data were available were similar from a length of about 370 mm and up. The difference in distributions occurred for fish with lengths less than 370 mm. This is almost certainly a sampling gear effect, as all earlier samples were taken from the fishery, which used gillnets with 10-cm stretch mesh webbing, while the 2003 samples included the catches from a 5-cm stretch mesh gillnet as well. It is assumed that if smaller-mesh gillnets had been fished in previous years a similar group of small humpback whitefish would have been observed.

During the September sampling event humpback whitefish appeared to be in low abundance throughout most of the Selawik River delta, except in one lake system in the northern part. Nine of the 12 humpback whitefish taken in the fall were caught in the lake. All were preparing to spawn as evidenced by the high GSI values of the two females and pearl tubercles on males and females. The other three humpback whitefish sampled in September were caught individually elsewhere in the delta, and were not preparing to spawn. All of the fish preparing to spawn were affected by fungus infections. Some infections appeared to be minor, covering two or three spots 1 cm or more in diameter, while others were severe, covering a third or more of the affected fish's body and penetrating through the skin into the musculature (Figure 20). Photographs of these fish were sent to the fish pathology laboratory operated by the Alaska Department of Fish and Game in Juneau for consultation. T. Meyers (ADF&G, Juneau, personal communication) responded that fungus infections in fish are usually caused by traumatic injuries of some sort and are commonly seen on salmon preparing to spawn. Observations of bruising in tissue underlying fungus infections support this suggestion, but it is unclear how such injuries could be inflicted. Broad whitefish and least cisco captured in the same location were not affected by fungus infection. Some local fishers were alarmed by the condition of these fish but others claimed to see fish in similar condition each fall at that site.

## **Summary**

Three species of whitefish were found to be relatively abundant in the Selawik River delta during 2003. Broad whitefish were the most common in subsistence catches, followed by humpback whitefish and then least cisco. The use of small-mesh gillnets in directed sampling activities revealed that least cisco were more abundant than subsistence harvests would indicate, but are missed because of the large-mesh gillnets used in that local fishery. Juvenile fish were rare in the catches, and most fish of all three species were mature. Otolith microchemical data showed that most broad whitefish and humpback whitefish migrate to marine environments during their first few years, which probably explains the scarcity of immature fish in samples from the delta. Most least cisco remained in freshwater throughout life, and it is likely that juveniles could be found in Selawik Lake, or other difficult-to-sample habitats, if sampled with appropriate gear. The high incidence of feeding for all three species, and the increase in size of broad whitefish and least cisco between June and September reveal the importance of the Selawik River delta as feeding habitat. Age distributions for all three species ranged much higher than minimum age of maturity, to maximum ages similar to those observed in other populations, indicating that survival is adequate and overfishing is currently not a

problem. All three species were much more abundant in June than in September. Since most fish in the area were found to be mature it is thought that a major component of the population present in June were migrating to distant spawning areas and not available to the fishery in September. The evidence from GSI data suggests that at least some mature broad whitefish and humpback whitefish do not spawn every year, but it appears that mature least cisco do spawn every year.

### Acknowledgements

This project was conducted by the U. S. Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office and the Selawik National Wildlife Refuge. The U.S. Fish and Wildlife Service, Office of Subsistence Management, provided funding support for this project through the Fisheries Resource Monitoring Program, under project number FIS 03-016. In addition, a number of individuals provided substantial logistical and field assistance that greatly enhanced the project operations. They include Ralph Ramoth Sr., Susan Georgette, Clyde Ramoth, Melissa Robinson, Pauline Ramoth, Lisa Fox, and Hannah Loon. Many others from the village of Selawik offered assistance and encouragement. This project would not have been possible without such broad community support, and it is appreciated. Finally, Chrissy Appodaca, Fred DeCicco, Susan Georgette, Polly Wheeler, and Jeff Adams reviewed drafts of this manuscript and provided comments that improved the final product.

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TABLE 1.—Fish species and number examined during the June and September sampling periods in the Selawik River delta during 2003.

Common name Species	Abbrev.	June	Sept.	Total
Broad whitefish Coregonus nasus	BWF	60	56	116
Least cisco Coregonus sardinella	LC	64	45	109
Humpback whitefish Coregonus pidschian	<b>HBWF</b>	53	12	65
Northern pike <i>Esox lucius</i>	NP		22	22
Longnose sucker Catostomus catostomus	LS		4	4
Inconnu (sheefish) Stenodus leucichthys	IN		3	3
Arctic grayling <i>Thymallus arcticus</i>	AG		1	1
Burbot Lota lota	BB		1	1
Total		177	144	321

TABLE 2.—A complete tally of number (and percent of annual sample) of whitefish during four years of sampling in the Selawik River delta.

Year	BWF	HBWF	LC	IN	Total
1985	275 (61%)	121 (27%)	45 (10%)	13 (3%)	454
1987	292 (62%)	131 (28%)	14 (3%)	31 (7%)	468
1993	290 (74%)	63 (16%)	27 (7%)	14 (4%)	394
2003	116 (40%)	65 (22%)	109 (37%)	3 (1%)	293
Total	973 (61%)	380 (24%)	195 (12%)	61 (4%)	1,609

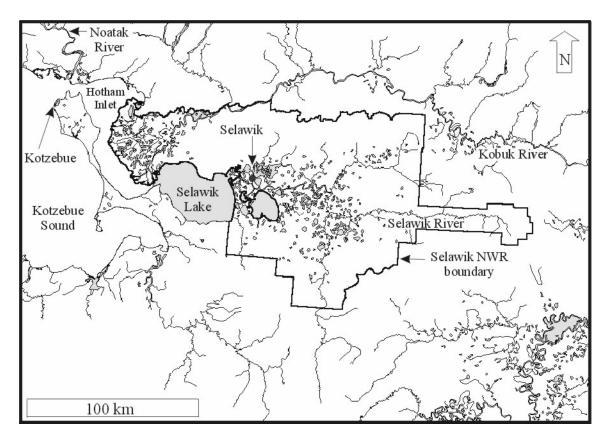


FIGURE 1.—The Selawik River drainage and surrounding area in northwest Alaska.

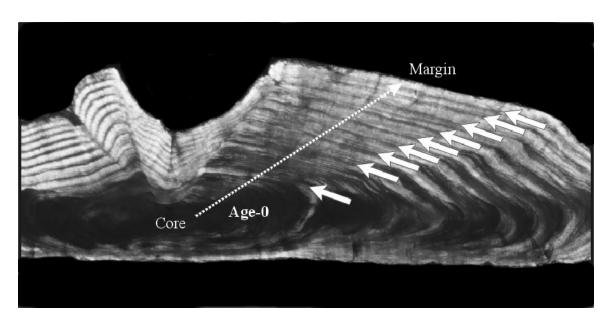


FIGURE 2.—Optical image of a thin-sectioned otolith (ear bone) with annuli identified with arrows. The dotted line illustrates the core-to-margin transects used for microchemical analyses.

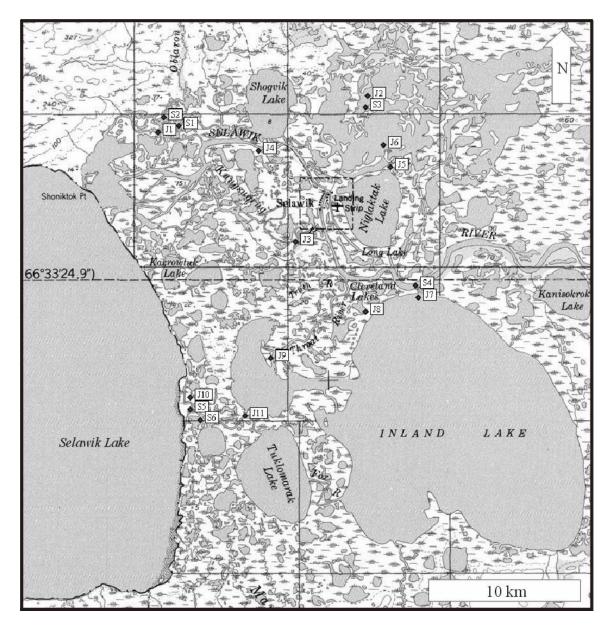


FIGURE 3.—Fishing site locations in the Selawik River delta in June (J#) and September (S#), 2003.

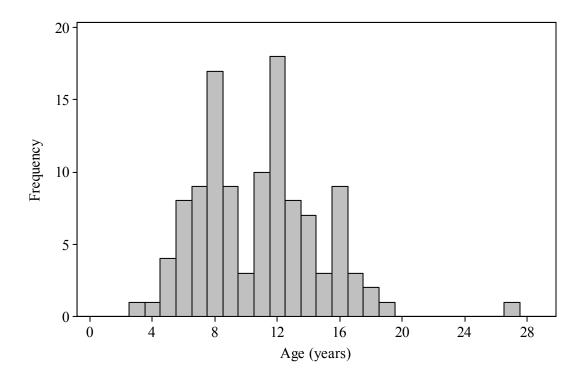


FIGURE 4.—Broad whitefish age distribution for samples collected in 2003 (n = 114).

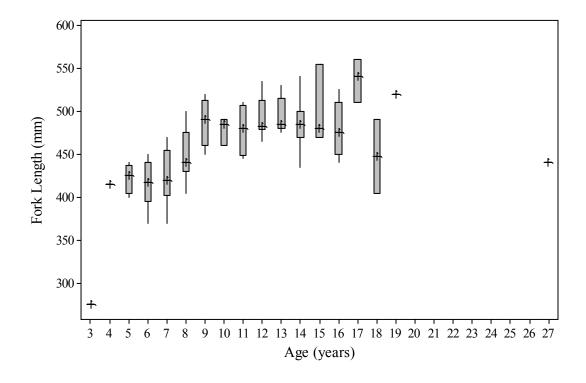


FIGURE 5.—Boxplot of broad whitefish length at age for samples collected in 2003 (n = 114). The crosses indicate the median length for each age category.

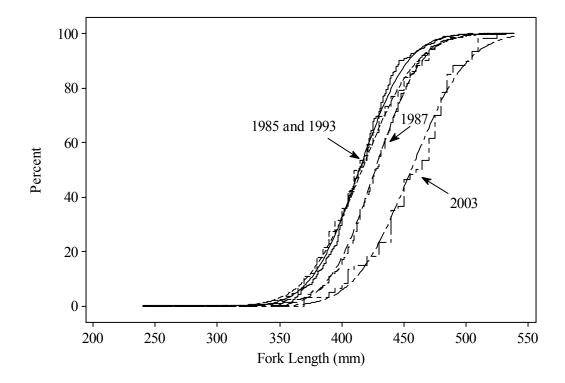


FIGURE 6.—Broad whitefish cumulative length distribution functions for samples collected in 1985 (n = 275), 1987 (n = 292), 1993 (n = 290), and 2003 (n = 116). The stepped line represents empirical values and the smoothed line is fit to the data.

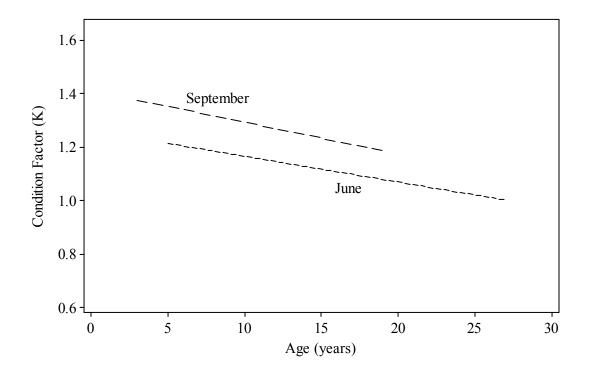


FIGURE 7.—Regressions of the condition factors (K) by age for broad whitefish from the June (n = 58) and September (n = 56) samples in the Selawik River delta, 2003.

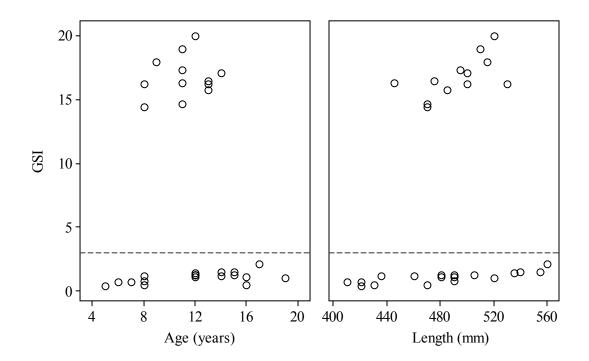


FIGURE 8.—Broad whitefish September GSI values plotted against age and length. Values below GSI = 3 (dashed line) come from nonspawning fish.

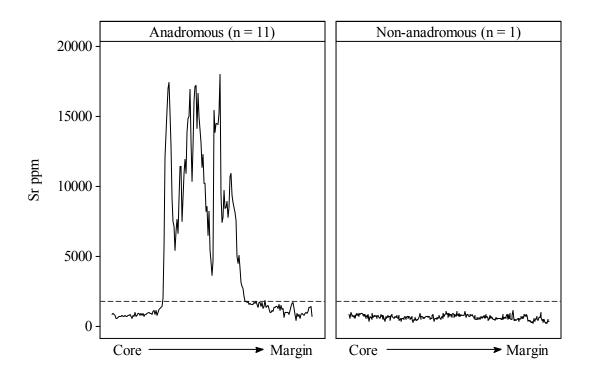


FIGURE 9.—Otolith Sr distribution in ppm along core- (precipitated when the fish was young) to-margin (precipitated when the fish was old) transects of representative anadromous and non-anadromous broad whitefish from the Selawik River delta, 2003. Strontium values above 1,750 ppm (dashed line) indicate migration into marine water.

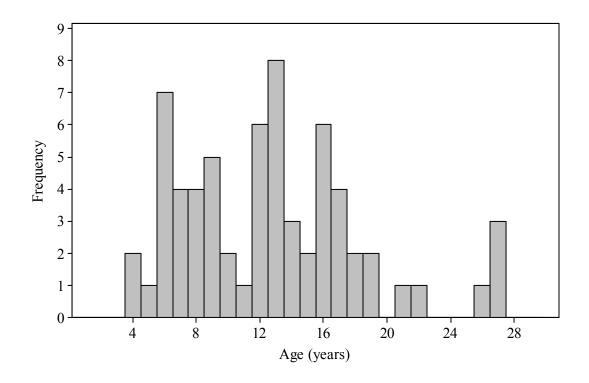


FIGURE 10.—Humpback whitefish age distribution for samples collected in 2003 (n = 65).

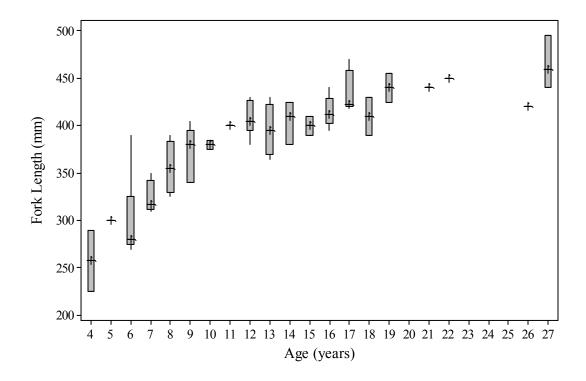


FIGURE 11.—Boxplot of humpback whitefish length at age for samples collected in 2003 (n = 65). The crosses indicate the median length for each age category.

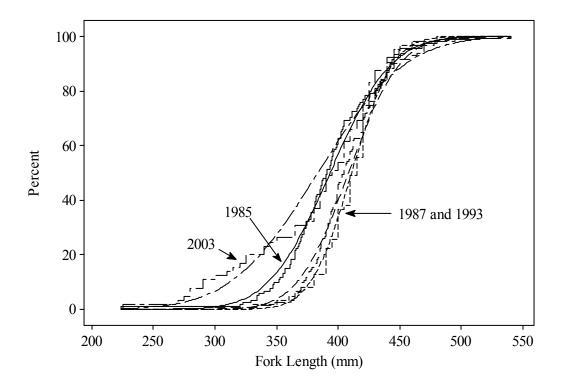


FIGURE 12.—Humpback whitefish cumulative length distribution functions for samples collected in 1985 (n = 121), 1987 (n = 131), 1993 (n = 63), and 2003 (n = 65). The stepped line represents empirical values and the smoothed line is fit to the data.

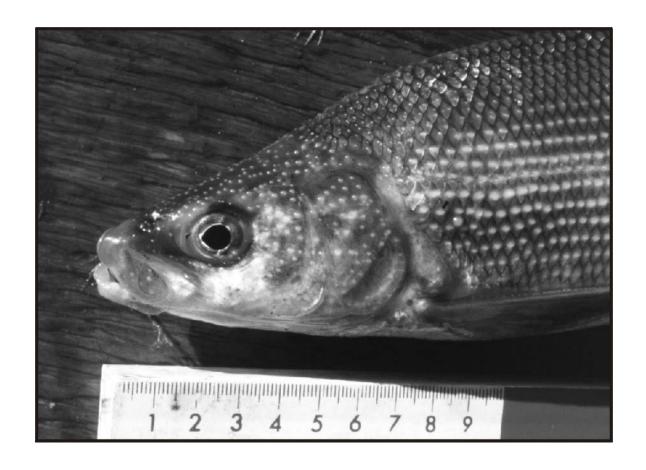


FIGURE 13.—Male humpback whitefish with pearl tubercles, bumps on scales and head, indicating preparation for spawning. The scale is cm.

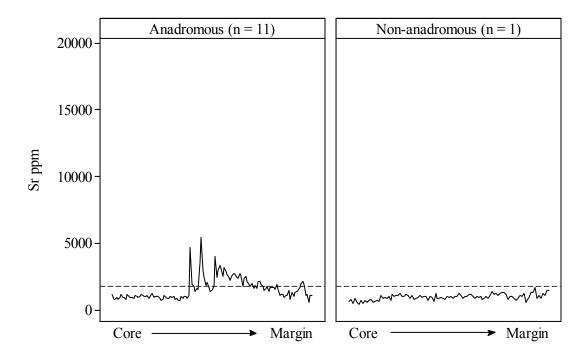


FIGURE 14.—Otolith Sr distribution in ppm along core- (precipitated when the fish was young) to-margin (precipitated when the fish was old) transects of representative anadromous and non-anadromous humpback whitefish from the Selawik River delta, 2003. Strontium values above 1,750 ppm (dashed line) indicate migration into marine water.

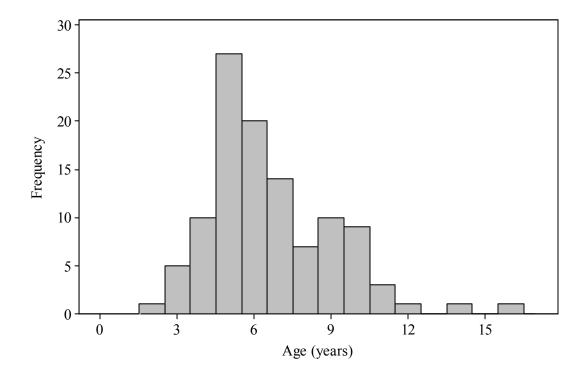


FIGURE 15.—Least cisco age distribution for samples collected in 2003 (n = 109).

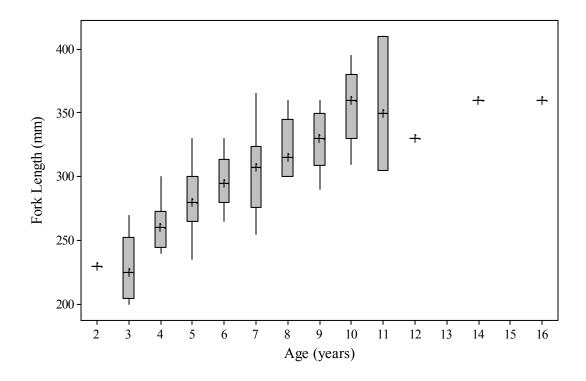


FIGURE 16.—Boxplot of least cisco length at age for samples collected in 2003 (n = 109). The crosses indicate the median length for each age category.

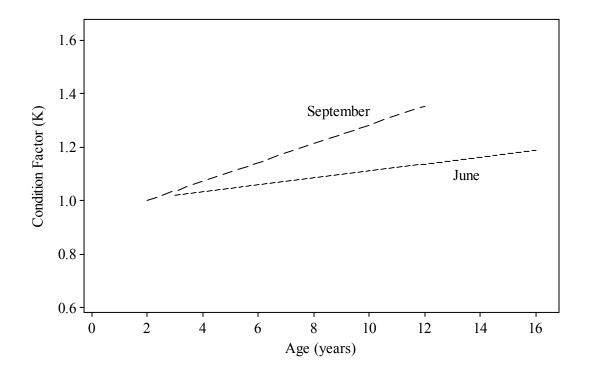


FIGURE 17.—Regressions of the condition factors (K) by age for least cisco from the June (n = 64) and September (n = 45) samples in the Selawik River delta, 2003.

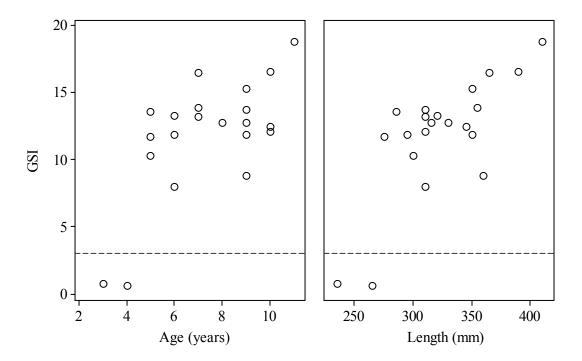


FIGURE 18.—Least cisco September GSI values plotted against age and length. Values below GSI = 3 (dashed line) come from non-spawning fish.

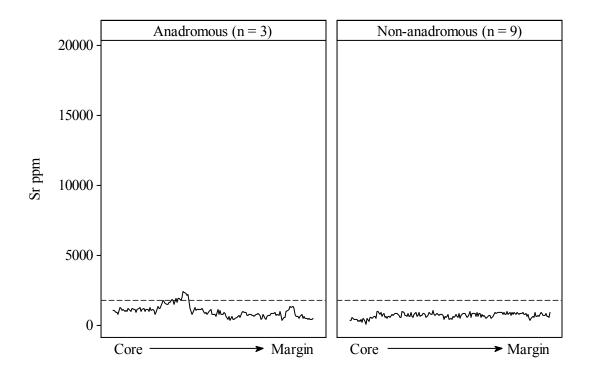


FIGURE 19.—Otolith Sr distribution in ppm along core- (precipitated when the fish was young) to-margin (precipitated when the fish was old) transects of representative anadromous and non-anadromous least cisco from the Selawik River delta, 2003. Strontium values above 1,750 ppm (dashed line) indicate migration into marine water.

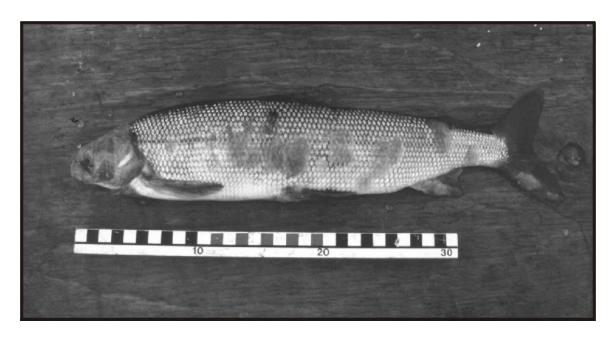


FIGURE 20.—Humpback whitefish with severe fungus infection. This fish was alive at the time of capture. The scale bar is in cm.